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DIVERSITY IN CENTRAL AUSTRALIAN LAND SNAILS (GASTROPODA: PULMONATA)

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Abstract

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Much of the land snail diversity in central Australia is due to camaenids (70 of 83 spp.). Many camaenid species have restricted distributional ranges so that, although land snail diversity in Central Australia is relatively high, local diversity is generally low. The fauna of the Krichauff Range in the Central Ranges is an exception to this general rule as the Finke Gorge National Park contains at least 25 species of snails, 30% of the central Australian fauna. Similar areas in the Central Ranges, such as the George Gill Range and eastern MacDonnell Ranges have a significantly lower diversity of land snails. It is postulated that high levels of diversity and endemicity in central Australian camaenids are the product of vicariance events related to Tertiary and Quaternary changes in climate.

Introduction

Over 80 species of land snails from eight families have been recorded from central Australia (Solem, 1989, 1991, 1993; Scott, in prep.). The land snail fauna is dominated by the families Camaenidae and Pupillidae *s.l.*, both of which are widespread across mainland Australia. Other families are represented in this area by no more than two species each. It has been suggested that the relatively small number of families in the central Australian fauna (compared with the greater complement in coastal areas) is the result of dispersal from coastal centres of origin to the interior, combined with the effect of filtering due to fluctuating climatic conditions (Solem, 1993). Problems arise, however, with dispersal hypotheses as explanations of the origin and distribution of organisms as they are *ad hoc* narratives used to describe specific cases and, as such, are generally untestable.

Hypotheses concerning vicariance biogeography provide alternative interpretations of distributions. In that model of historical biogeography, it is assumed that taxa and the areas they occupy have evolved together (Nelson and Platnick, 1981). Reconstruction of a phylogeny allows the reconstruction of the history of a region. Biogeographic hypotheses erected using data from one group of organisms can be tested with those from another. Land snails are excellent subjects for such biogeographic studies as they are 'vicariant conformers' (Springer, 1981: 230), responding rapidly to environmental disruptions (Gould, 1969).

Origins and diversification of the Central Australian land snail fauna

It has been suggested that many families represented in central Australia were Tertiary invaders from Asia and that the apparent reduction in diversity from north to south and from east to west is a result of dispersal from tropical centres of origin (Solem, 1959, 1992, 1993). The most diverse of those families, the Camaenidae, is postulated to have entered Australia in several waves (Solem, 1959, 1992, 1993; Bishop, 1981), the products of the earliest wave having the most extensive distribution and those of the most recent restricted to the eastern rainforests (Solem, 1959). This interpretation is based on the assumption of monophyly of American and Australasian camaenids but this assumption is probably incorrect (Scott, 1996). It is possible that the Australasian component of this family is closely related to the Asian Bradybaenidae (Scott, 1996) and is of Gondwanan origin (Scott, in press).

Central Australian camaenids show a high degree of regional endemism but two genera in the subfamily Sinumeloninae, *Sinumelon* and *Pleuroxia*, have ranges that extend beyond the Centre. Species of these genera occur in the Centre and in southern and parts of western Australia (Solem, 1992, 1993). This has been interpreted as the result of primary differentiation of ancestral taxa in the Centre, followed by southerly and westerly migrations to give rise to local radiations (Solem, 1992, 1993). Present distributions may, however, also be explained as the result of tectonic or climate-induced vicariance events which caused populations of ancestral taxa to become isolated and thus to give rise to modern taxa. Preliminary studies on the phylogeny and cladistic biogeography of the Sinumeloninae indicate that fauna of southern and western coastal areas was separated from that of central Australia early in the evolutionary history of the group (Scott, in prep.). Within the central Australian region, some montane areas, such as the Central Ranges, may have become isolated from adjacent areas not long after the Centre-SW split. Vicariance events causing disruptions of these magnitudes may have been associated with cyclical climate change in the Caenozoic, when periods of relative dryness associated with global cooling alternated with warm and humid pluvial stages. Alternation of arid grasslands and extensive water bodies in the plains and valleys may have presented significant barriers to formerly widespread snail taxa. Which of the two extremes may have played the more significant role cannot be determined, but they may have acted synergistically.

Congeners of the central Australian bulimulid *Bothriembryon spenceri* (Tate, 1894) are found in southern and western parts of the continent, as well as the south-eastern coast of Tasmania (Smith, 1992). There is generally little spatial overlap between the Camaenidae and Bulimulidae as camaenids do not occur in Tasmania or the extreme south-west of the mainland and *Bothriembryon* is not found in the north or east. However, although the distributions of *Bothriembryon* and the two camaenid genera, *Sinumelon* and *Pleuroxia*, do not correspond entirely, broad geographical congruence between the three genera is such that future phylogenetic and biogeographic analysis of one genus will provide a hypothesis available for testing with the other two genera.

Patterns of diversity in the Central Ranges land snail fauna

Almost half of the Central Australian species of land snail have been recorded from the Central Ranges (MacDonnell, Krichauff and George Gill Ranges) (Smith, 1992; Solem, 1993; Scott, in prep.), which cover 12% of the area of this region, while Finke Gorge, in the Krichauff Range, alone contains almost a third of the central Australian land snail species (Table 1). The snail fauna of the Central Ranges is well-known as collecting sites are readily accessible, but direct comparison between the Central Ranges and adjacent areas may present problems as sites further away from Alice Springs may have been less thoroughly explored.

Camaenid species comprise 66% of the land snail fauna of the Central Ranges and demonstrate a high level of endemism compared with species in other families (Table 2). The non-camaenid species of that fauna are largely widespread, shared with other parts of Central Australia and, in several cases, also with coastal areas.

The pattern of diversity demonstrated by camaenids in the Central Ranges can be seen in other areas such as the Kimberley and adjacent ranges (Solem, 1979, 1981a, 1981b, 1984b, 1985, 1988a, 1989). Many of these endemic species have narrow ranges which are usually allopatric to congeners (Solem, 1988b). This appears to be a common pattern among land snails (Solem, 1984c) and it is rare for two short-range Central Ranges endemics to occur sympatrically, although they are frequently found with other more widely-distributed species. Geographic ranges do not appear to be restricted by competition as they are never parapatric and, as narrow-range endemics do not come into contact with each other, there can be no evidence of repressive interactions.

Pleuroxia adcockiana (Bednall, 1894) is the sole representative of the genus in the Central Ranges and the edges of its distribution coincide with those of the Central Ranges biogeographical area. The four species of *Sinumelon* in this area are moderate-range endemics and divide the Central Ranges into four units: far western MacDonnell Ranges, Krichauff and James Ranges (*S. expositum* Iredale, 1937), near western MacDonnell Range and Alice Springs (*S. bednalli* Ponsonby, 1904), eastern MacDonnell Range (*S. dulciensis* Solem, 1993) and George Gill Range (*S. gillensis* Solem, 1993) (Solem, 1993).

The genera *Granulomelon* and *Semotrachia* show very high degrees of endemism. Three of five species of *Granulomelon* are found in the Central Ranges and two of those are known only from single localities, at opposite ends of Finke Gorge (Solem, 1993; Scott, in prep.). *Semotrachia* is an extremely diverse genus, with 18 of its 28 species known only from the Central Ranges (Solem, 1992; Scott, in prep.). Many (16) of these species are narrow-range endemics, confined to single gorges in the eastern and western MacDonnell Ranges, or from rock walls in the Krichauff, James and George Gill Ranges.

Combination of patterns of distribution from these species suggests that although the Central

Table 1. Land snail diversity in Central Ranges (data compiled from Solem, 1989, 1991, 1993; Scott, in prep.) ([a] total number of species recorded from the Central Ranges = 39; [b] total number of species recorded from central Australia = 83).

	No. of species[a]	% of species recorded from central Australia[b]
Western MacDonnell Range	23	27.7
Eastern MacDonnell Range	14	16.8
Krichauff and James Ranges	27	32.5
Finke Gorge	25	30.1
George Gill Range	9	10.8

Table 2. Land snail diversity at selected sites in the Central Ranges (sites are approximately equivalent in size) (data compiled from Solem, 1984a, 1989, 1991, 1993; Scott, in prep.)

	endemic camaenids	non-endemic camaenids	endemic others	non-endemic others
Krichauff Range				
Finke Gorge	7	4	0	14
W MacDonnell Range				
Glen Helen	1	3	0	12
Serpentine Gorge — Ellery Big Hole	1	3	0	5
Simpson Gap — Fenn Gap	2	3	0	6
Alice Springs	1	3	0	6
Eastern MacDonnell Range	4	4	0	6
George Gill Range	2	0	1	6

Ranges represent a coherent biogeographic unit, this unit can be divided into seven areas, each with its own evolutionary history. The Alice Springs region, eastern MacDonnell Ranges, Krichauff and James Ranges, and the George Gill Range each represent single areas, while the western MacDonnell Range is a composite of three sub-areas.

Evolution in the Central Ranges

The Central Ranges are subparallel strike ridges, running approximately east-west, and are composed principally of sandstone and quartzite with some dolomite and shale (Mabbutt, 1967; Thompson, 1991). The MacDonnell Ranges are divided into eastern and western components by the Todd River and the western range is separated from the Kriehauff and James Ranges immediately to its south by Missionary Plain. The Krichauff and James Ranges are continuous with the eastern MacDonnell Range as one arm of a geosyncline; the western MacDonnell Range forms the other arm (Thompson, 1981).

Extreme climate changes of the Tertiary are registered in the geomorphology of the Central Ranges. The ranges rise abruptly from plains and, in many areas, are capped with duricrust, indicating the pre-erosional valley floors of the Tertiary. Exposure of the mountain ranges and the subsequent cutting of gorges through the ranges has probably occurred only over the last 20 million years (Twidale, 1994). The presence of numerous watercourses, which cut across the ranges rather than run parallel to them, indicate the importance of water in producing this landscape. Several significant waterways are found in this area, including the Finke River and its tributaries in the western MacDonnell and Krichauff Ranges, and the Ross River in the eastern MacDonnell Range.

Coincidence of waterways with the limits of biogeographic areas suggests that rivers may have been important in the dissection and isolation of ancestral populations. Water-cut gorges and depositional plains provide evidence of significant pluvial phases, during which snails might have been restricted to montane islands.

Increasing aridity during glacial phases may have contributed to the isolation of populations and subsequent speciation (e.g. Haffer, 1982; Winter, 1988; Bush and Colinvaux, 1990) but the numerous short-range endemic land snails in otherwise contiguous mountain ranges suggest that it is the presence of water, rather than its absence, which is the most important factor in speciation here.

Implications for land snail conservation

Short-range endemic invertebrates are often neglected when areas are selected for conservation. Economic imperatives ensure that surveys focus on readily-observed and readily-identified taxa, such as vascular plants and vertebrates with little attention directed towards other organisms. As the range of a snail species may be less than 0.5 km^2 (Solem, 1988b), the inclusion of narrow-range invertebrate taxa in protected areas is as likely to be the result of good luck as it is of good planning. Awareness of the possible existence of such taxa combined with an understanding of the history of an area will greatly increase the chances of short-range endemics being located and subsequently protected from extinction.

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